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**Intermountain
Research Station**

Research Note
INT-420

February 1994

Genetic Variation in Susceptibility of Lodgepole Pine to Western Gall Rust in the Inland Northwest

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Abstract—Infection of a provenance-family test of lodgepole pine by western gall rust was 70 percent at age 11 years. The test provided data for determining geographic and elevation patterns of variation for infection, plus data to assess levels of variation among families. Susceptibility was highest in the western portion of the populations included in the test and decreased easterly. Susceptibility also increased slightly with elevation to about 1,300 m trailing off to 1,830 m. Family heritability was 0.57. This information can be incorporated into breeding programs.

Keywords: *Pinus contorta*, *Endocronartium harknessii*, geographic variation, disease resistance

Lodgepole pine (*Pinus contorta* Dougl.) is the most widely distributed conifer in western North America. Its natural range spans 33° latitude, 35° longitude, and over 3,900 m of elevation. It is the principal tree species on over 26 million ha of forest land in western Canada and the United States (Wheeler and Critchfield 1985). There are, however, some major pest problems associated with this species that could result in serious damage. One is the western gall rust, which is caused by *Endocronartium harknessii* (J. P. Moore) Y. Hiratsuka. Western gall rust is a common stem rust that occurs throughout lodgepole pine's natural range. The damage varies with region, size of tree, and climatic conditions (Dahms 1965; Peterson 1971; Powell and Hiratsuka 1973). The rust is considered a major disease (Hiratsuka and Powell 1976) in most areas, especially in plantations (Martinsson 1980; Powell and Hiratsuka 1973). Lodgepole pine in the Inland Empire—a large area encompassing northeastern Washington, Idaho north of the Salmon River, and western Montana—is severely damaged by western gall rust (Peterson 1961).

The objective of recent tree improvement programs is to take advantage of the fast early growth rate of lodgepole pine. New and faster growing populations are created by changing gene frequencies. However, because the variability of gall rust susceptibility of lodgepole pine within the region is largely unknown, more information is needed concerning how gall rust relates to lodgepole pine's genetic susceptibility to the rust.

Martinsson (1980) reported that high-elevation and high-latitude provenances of British Columbia were more susceptible to western gall rust. Yanchuk and others (1988) reexamined this material when the trees were older, and with several more provenances, and found the same relationship with elevation. Hoff (1992), on the other hand, found that the number of galls per tree decreased with increasing elevation. However, this test used artificial inoculation with western gall rust; the result could have been due to the amount of susceptible tissue available at the time of inoculation—that is, low-elevation provenances put on more growth than high-elevation provenances (Rehfeldt 1988).

The Inland Empire Tree Improvement Cooperative—whose members include industries, states, tribal councils, Federal Government, and universities—has established 20 plantations of lodgepole pine. One of these tests was established by the Forest Service at a site in northern Idaho and is surrounded by a natural stand that is heavily infected with western gall rust. The plantation became heavily infected. This provided excellent data on the variation of lodgepole pine in respect to natural infection by western gall rust. The objectives of this research are (1) to assess the geographical patterns of variation in lodgepole pine to susceptibility to western gall rust, (2) to assess variation among open-pollinated families of lodgepole pine to susceptibility to western gall rust, and (3) to provide a theoretical base for seed transfer, management, and

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tree improvement programs in respect to lodgepole pine's susceptibility to western gall rust.

MATERIALS AND METHODS

The provenance-family test plantation was planted during spring 1980 at the Lone Mountain tree improvement center 40 km north of Coeur d'Alene, ID. The site, at an elevation of 758 m, is flat with only slight undulations. The entire 65-ha site is surrounded by naturally regenerated lodgepole pine and ponderosa pine with a lesser mixture of grand fir (*Abies grandis*), Douglas-fir (*Pseudotsuga menziesii*), and western larch (*Larix occidentalis*). This two-layered natural stand has an overstory of mature or overmature scattered trees (remnants of harvest) and a lower layer of pole-size trees 6 to 9 m tall. Many of the lodgepole pine and ponderosa pine trees are infected by western gall rust.

The lodgepole pine plantation is situated in the southwest corner of the tree improvement site. The rectangular plantation measured 183 by 457 m, and the south and southwest sides are 6 m from the natural stand.

The seed came from 191 open-pollinated individual trees (families) from 30 localities (provenances) (fig. 1, table 1), throughout northern Idaho (north of the Salmon River) and northeastern Washington.

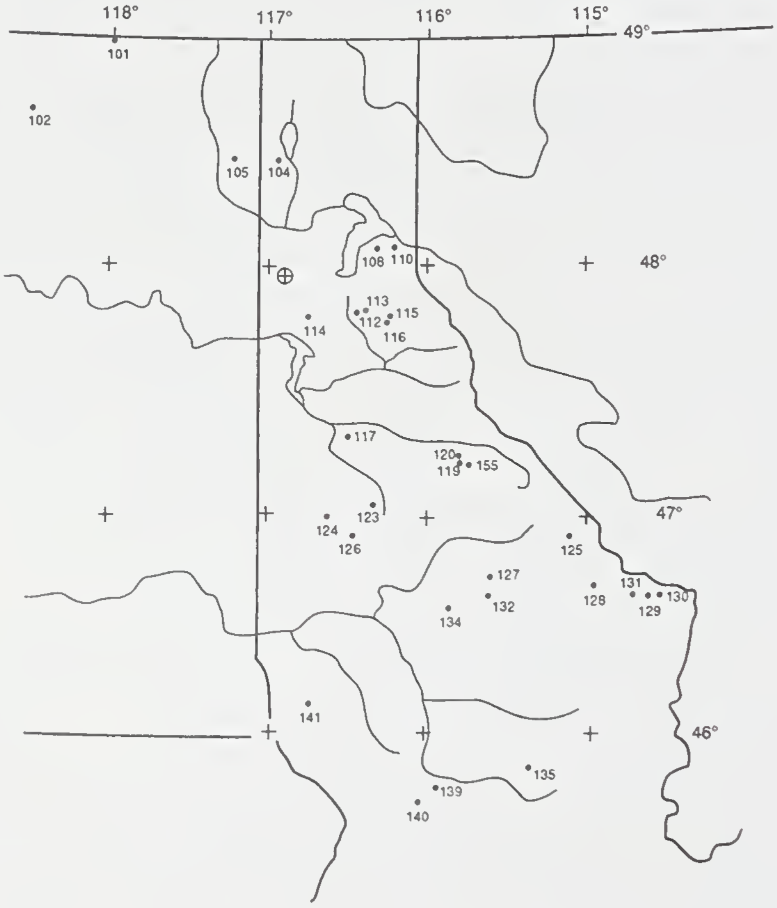


Figure 1—Number and locations of populations of lodgepole pine that were included in this test. The + represents location of test plantation.

Table 1—Elevation and habitat type of lodgepole pine provenances and 11-year provenance means for western gall rust (WGR)

Provenance number	Name	Elevation	Habitat type	Mean-WGR
		Meters		*Percent*
101	American Fork	1,128	[1]1	82
102	Timber Ridge	1,372	5	81
104	Squaw Valley	762	4	51
105	Cee Cee Ah Cr.	1,189	2	77
108	Johnson Creek	1,067	3	79
110	Deer Creek	1,555	6	61
112	Tenderfoot	1,220	2	54
113	Barney Creek	1,220	4	85
114	Kelly Mt.	854	2	72
115	Short Creek	1,372	4	80
116	Fernan	1,524	4	76
117	St. Maries	1,372	3	84
119	Kelly Hill	1,372	2	76
120	Kelly Creek	1,311	3	84
123	Emerald Creek	915	3	81
124	Bonami	1,159	3	78
125	Birch Hill	1,677	9	60
126	Erickson Md.	854	2	67
127	Tumble Creek	1,311	2	80
128	Toboggan Ridge	1,829	7	69
129	Lolo Pass	1,707	6	62
130	Pack Pole	1,585	7	43
131	Fox Creek	1,524	5	69
132	Oxford Meadow	1,159	3	71
134	Poorman Creek	1,006	3	62
135	Queen Creek	1,372	2	80
139	Merton Creek	1,402	2	66
140	Cold Springs	1,524	2	71
141	Deer Creek	1,520	2	77
155	Shoe Pac	1,524	3	78

[1] Habitat types are as follows:
1 = *Pseudotsuga menziesii-Physocarpus malvaceus*
2 = *Abies grandis-Clintonia uniflora*
3 = *Thuja plicata-Clintonia uniflora*
4 = *Tsuga heterophylla-Clintonia uniflora*
5 = *Abies lasiocarpa-Clintonia uniflora*
6 = *Abies lasiocarpa-Menziesia ferruginea*
7 = *Abies lasiocarpa-Vaccinium scoparium*
9 = *Tsuga mertensiana-Xerophyllum tenax.*

The seedlings were grown at the Forest Service nursery at Coeur d'Alene, ID, in 66-cm^3 plastic containers and planted at the Lone Mountain plantation site in May 1980 just prior to their second growing season. The experimental design used was a randomized complete block with five replications (blocks). The plan called for eight progeny of each family per replication as single-tree plots. However, this varied from one to 14 (average of about six).

In June 1991, inspections of each tree in the plantation yielded the infection data. If a tree had at least

Table 2—Outline of analysis of variance and covariance

Source of variation	d.f.	Expected mean squares[1] or mean cross-products
Replications (R)	4	$\sigma_e^2 + k_1\sigma_{rf}^2 + k_2\sigma_{rp}^2 + k_3\sigma_r^2$
Provenances (P)	29	$\sigma_e^2 + k_4\sigma_{rf}^2 + k_5\sigma_{rp}^2 + k_6\sigma_f^2 + k_7\sigma_p^2$
R x P	116	$\sigma_e^2 + k_8\sigma_{rf}^2 + k_9\sigma_{rp}^2$
Families/P	161	$\sigma_e^2 + k_{10}\sigma_{rf}^2 + k_{11}\sigma_f\sigma$
R x families/P	644	$\sigma_e^2 + k_{12}\sigma_{rf}^2$
Error	4,822	σ_e^2
Total	5,776	

[1] σ_e^2, within-plot variance; σ_{rf}^2, family x replication variance; σ_f^2, family-within-provenance variance; σ_p^2, provenance; σ_{rp}^2, variance due to provenance x replication interaction; σ_r^2, replication variance; $k_1 = 6.38$; $k_2 = 48.07$; $k_3 = 1{,}151.5$; $k_4 = 6.27$; $k_5 = 38.84$; $k_6 = 30.11$; $k_7 = 190.89$; $k_8 = 6.07$; $k_9 = 37.77$; $k_{10} = 6.31$; $k_{11} = 30.26$; $k_{12} = 5.97$.

one gall it was tallied as 1. If there were no galls the tally was 0. Infection percentages were calculated from this 0, 1 data.

Table 2 includes the analysis of variance and covariance models and expected mean squares and mean cross products. We assumed the variance and covariance components for open-pollinated families within provenances would estimate one-quarter of the additive genetic variance and covariance (Wright 1976). Because of unequal plots, family mean (h_f^2) heritability was estimated as described by Yanchuk and others (1988):

$$h_f^2 = \frac{\sigma_f^2}{\dfrac{\sigma_e^2}{k_{11}} + k_{10}\dfrac{\sigma_{rf}^2}{k_{11}} + \sigma_f^2}$$

using notations defined in table 2. We obtained *k* values (table 2) from a least-squares analysis on individual trees assuming a completely random model. Sums of squares and expected mean squares were analogous to SAS Type I (SAS 1985).

Table 3—Mean square (MS), variance components (VC), percentage of variance component, and estimates of heritability (h^2) for infection of lodgepole with western gall rust

Source of variation	d.f.	MS	VC	%VC
Replications (R)	4	5.086	0.00423	2.24
Provenances (P)	29	1.908	0.00764	3.69
R x P	116	0.204	0.00066	0.32
Family/P	161	0.425	0.00814	3.93
R x family/P	644	0.179	–0.00120	0.00
Error	4,822	0.187	0.18650	90.02
Total	5,776			100.00
h_2 family = 0.57				

Simple and multiple regression models were used to relate the rust variables to elevation and geographic location of seed origin. The independent variables were elevation, latitude, longitude, northwest departure and southwest departure, habitat type, and miles from the test site. We added squares of independent variables to accommodate the possibility of nonlinear patterns of variation. We included 12 independent variables, not including habitat type, in a stepwise regression for maximizing R^2 (SAS 1985).

RESULTS AND DISCUSSION

Variation in susceptibility of lodgepole pine to western gall rust varied greatly among provenances and families. The infection means of provenance and family range from 43 to 85 percent and from 17 to 97 percent, respectively, with a mean of 71 percent.

Analysis of variance indicates that differences in infection means among provenances and among families in provenances were statistically significant ($p < 0.01$) (table 3). The effects of provenances and families in provenances accounted for 3.7 and 3.9 percent of the total variance (table 3), respectively. Variance components are shown in table 3. The heritability based on family mean within populations was 0.57. This relatively high heritability would indicate that gains in resistance to gall rust should be fairly easy to achieve.

Actual gall rust infection by seed source is shown in figure 2. Simple regression (R^2) of western gall rust infection was elevation at 0.01, latitude at 0.02, longitude at 0.16, distance from plantation site at 0.05, and habitat type at 0.20. The only strong association was with habitat type. The best fit stepwise multiple regression model:

Intercept	=	7.167648
ELEVATION	=	0.034018
ELEVATION^2	=	–0.000368
LATITUDE	=	–0.235745
NORTHWEST^2	=	0.000000132
DISTANCE^2	=	0.000005838

excluding habitat type, yielded an R^2 of 0.41. Figure 3 shows predicted values derived from this regression model for a constant elevation (average elevation for all stands). The lines contact equal predicted values. The distance between contour lines equals ½[lsd(0.2)]. Thus, distance equivalent to two contour lines differs by a probability of about 0.2. This analysis revealed a weak trend of decreasing infection toward the east. Generally, these data agreed with Hoff's (1992) data for a test of lodgepole pine artificially inoculated with western gall rust. However, in the Hoff test, number of galls per tree was used because the degree of infection was so high that differences among provenances was nonsignificant.

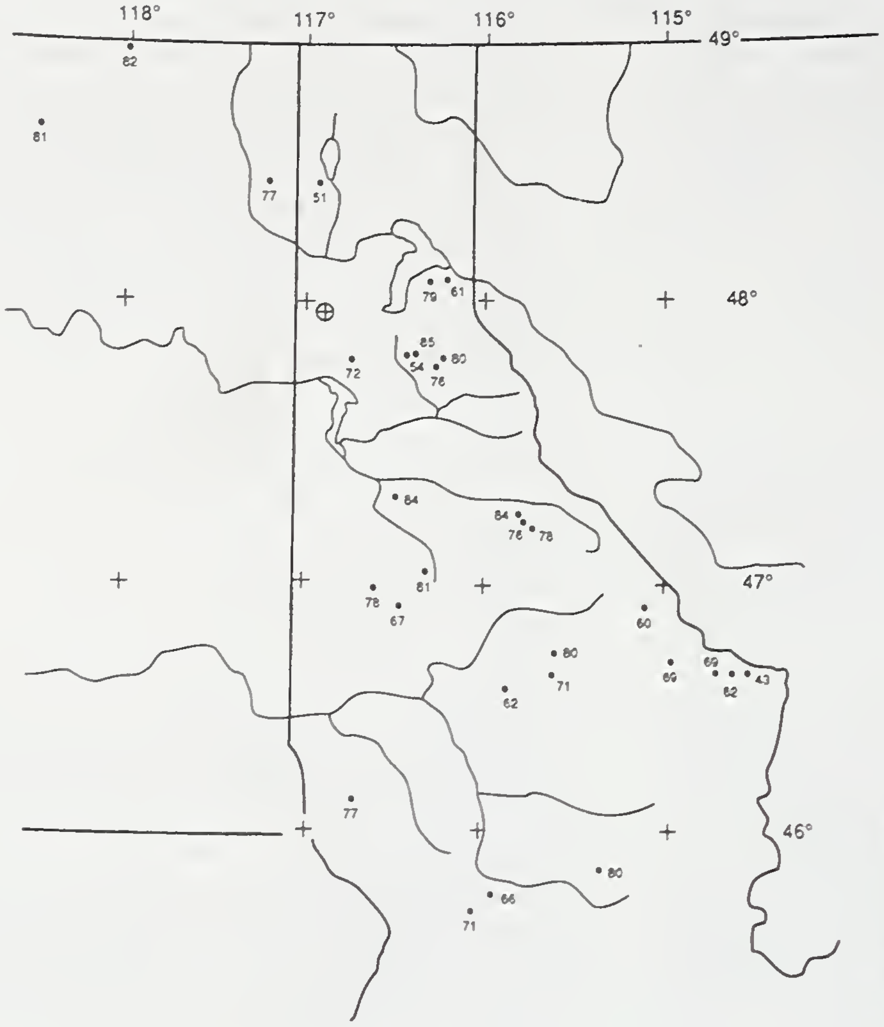


Figure 2—Level of infection of populations of lodgepole pine to gall rust. Numbers represent actual percentage of trees with galls. The + represents location of test plantation.

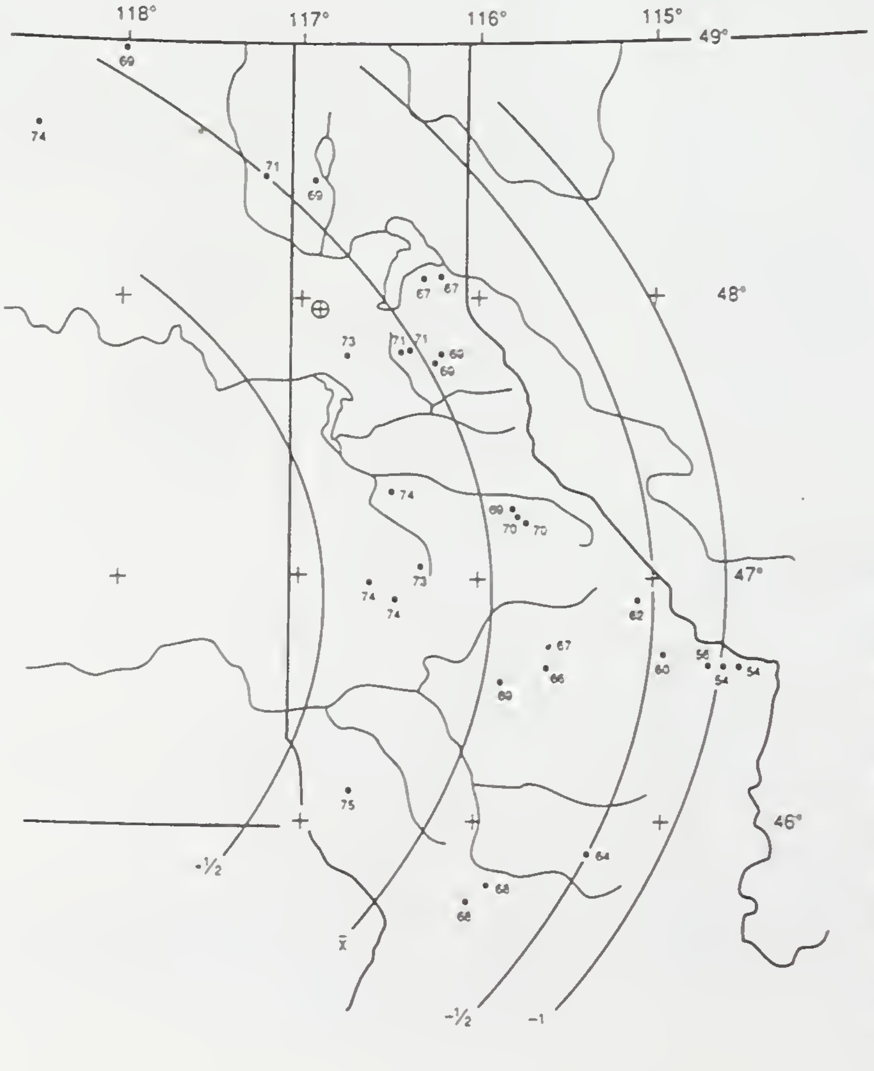


Figure 3—Level of infection of populations of lodgepole pine to gall rust. Numbers represent predicted values at the mean elevation of all populations (1,311 m). Contour lines represent lines of equal performance. The interval between contour lines equals ½[lsd(0.2)], and lines represent positive or negative deviations from the mean value of all populations.

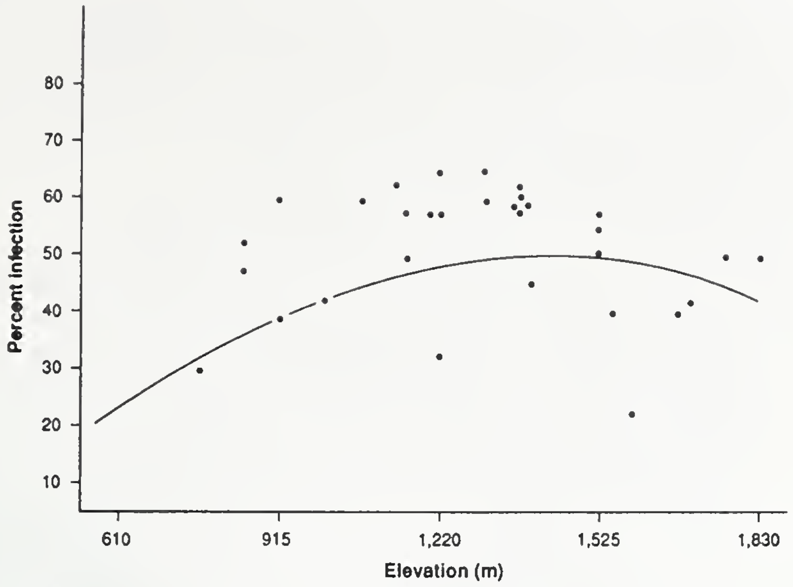
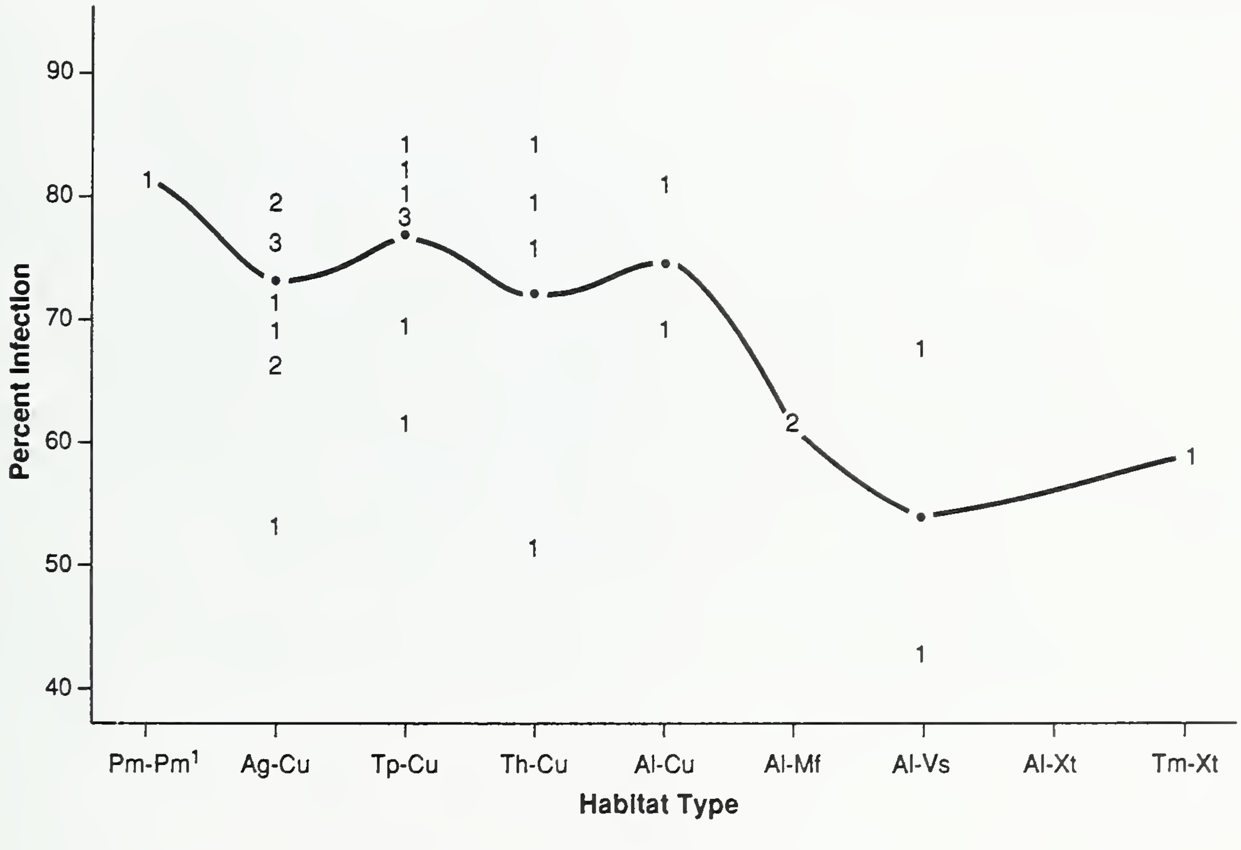


Figure 4—Level of infection of populations of lodgepole pine to gall rust. Dots represent actual percentage of infection. Line is fitted from multiple regression holding latitude, longitude and distance from source of inoculum constant (at average of each).

A slight trend of increasing infection occurred with increasing elevation (fig. 4), from elevation 854 m to about 1,300 m trailing off from there to elevation 1,830 m. The line indicates predicted values at constant values (average) for the other environmental values. In Hoff (1992), the number of galls decreased with increasing elevation.

The level of infection was also related to the effect of habitat types as indicated in figure 5. The three cold-dry habitats from high elevation had lowest level of infection. One of the cold-wet habitat groups also had low infection. However, the other cold-wet group from high elevation had high infection. Infection levels in all the warm-wet habitat type groups were high. Most surprising, infection was also high in the warm-dry habitat type.

The provenance data are in general so variable with only slight trends that it does not appear necessary, at this time, to attempt to select for more resistant provenances or be concerned about seed movements within the test area.



¹Pm-Pm = *Pseudotsuga menziesii-Physocarpus malvaceus* warm-dry
Ag-Cu = *Abies grandis-Clintonia uniflora* warm-dry
Tp-Cu = *Thuja plicata-Clintonia uniflora* warm-wet
Th-Cu = *Tsuga heterophylla-Clintonia uniflora* warm-wet
Al-Cu = *Abies lasiocarpa-Clintonia uniflora* cold-wet
Al-Mf = *Abies lasiocarpa-Menziesia ferruginea* cold-wet
Al-Vs = *Abies lasiocarpa-Vaccinium scoparium* cold-dry
Al-Xt = *Abies lasiocarpa-Xerophyllum tenax* cold-dry
Tm-Xt = *Tsuga mertensiana-Xerophyllum tenax* cold-dry

Figure 5—Level of infection of populations of lodgepole pine to gall rust plotted against habitat type. Numbers represent the number of populations with the same percentage. Line connects mean infection per habitat.

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